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Food consumption and seasonal variation in the diet of the aardwolf *Proteles cristatus* in southern Africa

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Abstract

Investigated were the food and foraging activity of twelve free ranging adult aardwolves *Proteles cristatus* and their cubs. For most of the year aardwolves are nocturnal and feed almost exclusively on the harvester termite *Trinervitermes trinervoides* (Sjostedt). During winter however, it is usually too cold for termites to forage at night, so the aardwolf becomes more diurnal and supplements its diet by feeding on another harvester termite *Hodotermes mossambicus* (Hagen), which is mainly active by day

and during the winter. Nevertheless, the aardwolf still suffers a food shortage during winter. This is evident from the weight loss (up to 20 % of body weight) experienced by all animals during this period. It is argued that the aardwolf's distribution across Africa is determined by the availability of those *Trinervitermes* species which are active throughout most of the year.

Introduction

The aardwolf *Proteles cristatus* is one of the most highly specialised carnivores in existence (KRUUK and SANDS 1972). Not only does it feed almost exclusively on termites but, throughout its African distribution, it feeds primarily on a few species of the genus *Trinervitermes*. The particular species changes as one moves across Africa, with *T. trinervoides* being the main species selected in South Africa (COOPER and SKINNER 1979). Two other predominant species have been found in the aardwolf's diet in Botswana/ Zimbabwe (SMITHERS 1983) and in East Africa (KRUUK and SANDS 1972). These three species appear to be ecological equivalents and are characterised by a few very important features. These are: (i) that they are each the only local species of termite which regularly harvests/forages for dry grass in dense concentrations and completely exposed on the soil surface; (ii) they are active for most of the year (KRUUK and SANDS 1972); and (iii) like all other nasute termites (Nasutitermitinae), they posses a highly effective means of chemical defence. The soldiers have well developed frontal glands from which they can squirt very sticky and noxious terpene-based secretions (PRESTWICH 1983; BRAEKMAN et al. 1984). These secretions appear to be highly successful in deterring attack from ants (LONGHURST et al. 1978, 1979), which are believed world-wide to be the major predators of termites (EISNER et al. 1976; DELIGNE et al. 1981), as well as most myrmecophagous (ant- and termite-eating) mammals (LUBIN and MONTGOMERY 1981; REDFORD and DOREA 1984).

It appears therefore that the chemical defence of these termites is so successful, that during their development the harvesters were able to forego the protection of the mud galleries used by most other termites and forage quite exposed on the soil surface (KRUUK and SANDS 1972). RICHARDSON (1985) has therefore suggested that the ability of the aardwolf to tolerate these terpene secretions must be its most significant adaptation, as this has made these termites readily available to the aardwolf and virtually without competition from any other mammal (KINGDON 1971; KRUUK and SANDS 1972; MELTON 1976). Having this ability, the aardwolf has developed a number of more obvious physical adaptations like a very broad tongue and palate, large salivary glands and well developed senses of smell and hearing (FLOWER 1869), which have enabled it to become extremely adept at feeding almost exclusively on this one food source. KRUUK and SANDS (1972) have suggested that it is this extreme specialisation of the aardwolf which is responsible for its being absent from West and Central Africa. Harvesting species of *Trinervitermes* are present in these more wooded regions, but they appear to be less suitable for aardwolf predation, being less common and not regular foragers throughout the year (SANDS 1961; OHIAGU 1979). This hypothesis therefore implies a very strong dependence by the aardwolf on having a harvesting *Trinervitermes* species as a regular food source throughout most of the year. The aim of the present paper is to test this hypothesis by investigating the aardwolf's dependence on *T. trinervoides* as a food source in the northern Cape of South Africa, and to relate its seasonal availability to aardwolf foraging activity and body weight during the year.

Materials and methods

The study was carried out on Benfontein (28°50′ S, 24°50′ E), an 11,300 hectare (ha) game farm near Kimberley, South Africa (Fig. 1). This is a semi-arid region which experiences large temperature fluctuations on both a daily and a seasonal basis. The winter months (May to August) are typically dry

Fig. 1. The farm Benfontein showing the main study area and the more important geographical features

with no cloud cover, so the days are frequently warm (regularly over 20 °C), while at night the temperature may fall below zero. The mean annual rainfall is 437 mm (Weather Bureau, Pretoria).

The main study area, of 2015 ha, lies in the eastern half of Benfontein and follows a gradual incline from a pan basin in the north-west to an area of Kalahari thornveld, which is the only area with trees *(Acacia erioloba)*, in the south-east. The slopes in between are dominated by various perennial grasses and Karoo shrubs, particularly *Pentzia* spp. Due to periodic waterlogging of the soil, mounds of *T. trinervoides* are completely absent from the pan basin. They are present throughout the remaining parts of the study area, and are larger and more abundant in areas with the densest grass cover.

All observations were made from a four-wheel-drive vehicle. Aardwolves were followed at very slow speed, at a distance of 15–30 m. Visual contact was maintained by keeping an animal in the headlights of the vehicle, or following it with the beam of a spotlamp mounted above the driver's window. All observations were recorded on a pocket dictaphone. The aardwolves were undisturbed

by the spotlamp or by the sound of the human voice. Binoculars (10×40) were used for observing them at a distance.

The resident aardwolves of five different territories were followed between July 1981 and September 1984. Individual recognition was aided by fitting eleven of the adults and seven of the cubs either with light-weight collars made from sterkolite (Sterkolite, Johannesburg) or, during the last year of the study, with radio-collars (seven adults and one cub). All collars had small coloured reflectors riveted to them to facilitate recognition of the bearer. Uncollared aardwolves were identified by natural earmarks and their stripe patterns. In order to fit the collars, aardwolves were immobilised, using either blowdarts or a dart gun (RICHARDSON 1983). Various body measurements were taken from the recumbent animals.

Nomination of a focal animal was done on a rotational basis in order to obtain data on each pair's territory every year. However, in order to get more complete data on breeding and feeding activities, observations were concentrated on two pairs of aardwolves, sometimes to the detriment of obtaining data on the other pairs. Aardwolves were usually followed from the time they left the den, until an hour or two after midnight. If one had already left the den, or was lost while being followed, then the study area was searched until it, or another aardwolf, was found.

During winter, because aardwolves were usually active for only a few hours in the late afternoon and early evening, it was frequently possible to follow them until they retired. However, over the rest of the year aardwolves were usually active all night. On these occasions, observations were usually terminated when an aardwolf lay down, or had covered most of its territory. During monthly "all-night studies", an aardwolf was observed for its entire period of activity.

Mapping

The method used to plot the movements of aardwolves was based entirely on the use of 420 colour-coded stakes, which were placed throughout the five aardwolf territories. Stakes were located at most dens and middens and as landmarks in areas in between. Observations of aardwolves were made whenever one passed near a stake, changed direction, or when there was a noticeable change in social or feeding behaviour. For each observation the aardwolf's distance and bearing to the nearest marker was recorded. Distances of over 30 m were estimated to the nearest 10 m. These data were used to calculate the coordinates of the aardwolf's position. From September 1982 to July 1984 all data were computerised and analysed according to a grid matrix of 100×100 m (1 ha) cells.

Feeding

Two categories of feeding data were collected: food type, and a relative measure of feeding intensity. The food type was almost invariably one or other of two species of termites – *Trinervitermes trinervoides* or *Hodotermes mossambicus*. These were easily identified by driving to where an aardwolf had just feed and shining a hand-held spotlamp at the ground. *Trinervitermes* are small, orange-coloured termites that feed in very dense concentrations, whereas *Hodotermes* are very much larger, nearly black in colour and forage in a more widely spaced fashion.

Feeding intensity was recorded on a scale of one to three. "One" was recorded if an aardwolf had fed on termites once, or only a few times since the last observation. "Two" was recorded if the aardwolf was feeding quite frequently, but still spent >50 % of the time walking. "Three" was recorded if an aardwolf spent more time feeding than walking. The feeding data were analysed assuming a uniform speed of movement during each observation period (see later) and were allocated to each hectare in proportion to the time spent there. Thus the relative feeding value per hectare was derived by multiplying the feeding intensity (0, 1, 2 or 3) by the time spent in that hectare. The estimation of the feeding intensity was clearly subjective, but the results were highly correlated (see later) with those of the detailed feeding analysis recorded during the all-night studies.

On these nights, in addition to recording the above data, each observation of feeding or walking was timed (with a stopwatch) during alternate 15 min periods. This was achieved with relative ease because the average feeding bout lasted over 20 sec (RICHARDSON 1985), so the spells of feeding and walking fell into quite discrete periods and were easily recorded. It was assumed that the feeding behaviour during the 15 min periods of detailed observations was, taken over the whole night, the same as during the "off" periods. These data then provided information on the total time spent feeding per night.

Faecal analysis

Fresh aardwolf faeces were collected approximately every two weeks during the last two years of the study. They were collected from middens in three different territories. An attempt was always made to collect a whole defaecation and the most recent one present. They were collected in a paper bag, labelled and later sun-dried. A total of 136 defaecations was collected.

Each sample was first oven-dried at 80 °C for 24 hours, then gently crushed with a pestle and

mortar till the contents could spread evenly. A rough estimate was then made of the proportion, by volume, of *Trinervitermes* to *Hodotermes* present. These termites are easily identified, as the heads of both soldiers and workers persist in the faeces and are very different in terms of size, shape and colour.

During the all-night studies an attempt was made to collect every defaecation of the animal being followed, as well as the first defaecation of the following night. These faeces were processed in the same way as above. In addition, an estimate of the total number of termites in one complete set of faeces was made in order to calculate the total number eaten per night. In doing this count, the first defaecation of that night was excluded and replaced by the first of the following night. The analysis was done by taking small samples from each defaecation and counting the total number of soldier's heads – which are more easily identified than the worker's heads and may also survive better (LUBIN and MONTGOMERY 1981). These samples were recorded by weight as a proportion of the whole defaecation.

Climatological data

The Kimberley airport is about 5 km west of Benfontein, so the daily maximum and minimum temperatures were taken from its weather station. During the last two years of the study the ambient temperature in the field was also recorded. To do this a thermometer on a foam rubber base was placed on the back of the truck and readings were taken periodically through the night.

Results

Foraging behaviour

The data on the foraging behaviour of aardwolves were collected while following 12 adults and 18 cubs. The times spent following these animals and the distances covered are summarised in Table 1.

Table 1

Distance and time spent following 30 aardwolves between September 1982 and July 1984

Name	Territory[1]	Sex	Days	Time[2] h	Distance km
Achilles	A	M	46	80.63	175.88
Seven Winds	A	F	42	109.23	160.47
William Tell	WT	M	29	37.43	71.98
Nausicaa	WT	F	28	27.82	48.38
Errol Flynn	EF	M	20	17.43	29.19
Muses	EF	M	15	15.02	28.51
Zebra	EF	F	16	18.00	31.14
Robin Hood	RH	M	18	21.83	37.48
Maid Marion	RH	F	23	20.53	30.03
Telemachus[3]	RH	M	8	7.73	10.87
Cyclops	C	M	9	9.95	17.51
Galatea	C	F	15	16.78	25.25
Adults Total	(n = 12)		269	382.96	666.69
Cubs Total	(n = 18)		68	51.82	69.10

[1] Territories are named after the initials of the resident male. – [2] Time does not include rest periods. – [3] Sub-adult which did not leave his natal territory.

Aardwolves are almost exclusively solitary foragers (KRUUK and SANDS 1972; RICHARDSON 1985), and feed by walking around their territories and stopping to lick up termites whenever they locate them. Thus their average foraging speed is directly related to the supply of termites available (Table 2). The table shows that they walk at an average speed of 2.3 km/h when they are not feeding, at 1.0 km/h when they are feeding at maximum intensity, and at regular intermediate speeds for feeding levels in between. This therefore justifies the methods which assume a uniform speed of movement during each observation.

Table 2

Characteristics of foraging aardwolves while feeding at different intensities

Relative Feeding Intensity	Distance km	Time h	Speed km/h
0	346.9	151.7	2.3
1	137.5	69.0	2.0
2	122.4	79.0	1.5
3	129.1	134.1	1.0
Total	735.9	434.7	1.7

Most of the detailed observations of feeding behaviour were recorded during the all-night studies. The results of the 13 nights that were successfully completed (one with no feeding), are summarised in Table 3. In this table the original values (every alternate 15 min) are given for the number of termite patches utilised, so they should be doubled to get the values per night. The correlations (values per ha) between the relative feeding value and the actual time spent feeding are also presented. On all nights the correlation was highly significant (p<0.01).

Table 3

Foraging data for the all-night studies

Name	Date	Max T °C	Dist. km	No. of Termite Patches	Food	Relative Feeding Value vs Total Feeding Seconds/ha		
						r^1	n	p
				Summer				
Seven Winds	1. 12. 82	33.0	8.2	286	*T*	0.66	45	<.001
Seven Winds	2. 2. 83	24.3	12.1	296	*T*	0.83	56	<.001
Seven Winds	3. 3. 83	28.0	11.7	340	*T*	0.54	56	<.001
Seven Winds	19. 1. 84	35.0	10.1	150	*T*	0.75	46	<.001
Seven Winds	14. 3. 84	30.6	8.2	303	*T*	0.73	48	<.001
Achilles	20. 1. 83	38.2	12.2	154	*T*	0.66	50	<.001
Achilles	11. 4. 84	23.3	8.0	210	*T*	0.67	40	<.001
Apollo	22. 2. 84	36.0	10.5	396	*T*	0.79	38	<.001
				Winter				
Achilles	24. 6. 84	18.9	6.2	56	*T*	0.74	25	<.001
Achilles	22. 6. 83	21.4	24.3	59	*.7T .3H*	0.42	48	<.003
Seven Winds	21. 7. 83	24.4	8.2	285	*.6T .4H*	0.60	38	<.001
Seven Winds	16. 5. 84	24.3	6.2	396	*.1T .9T*	0.80	33	<.001
Seven Winds	11. 5. 83	15.6	3.2	–	–	–	–	–

^{1} r = Spearman rank correlation coefficient.

The regression between the total values of these same two measures of feeding per night, is presented in Fig. 2. Here again there is a highly significant correlation (p<0.001) between the relative and actual values of feeding. These results indicate that the relative feeding data are reliable and can therefore be used to determine feeding values throughout the year.

In Fig. 3 the total amount of feeding on *Trinervitermes* is plotted against the maximum temperature for that day. The data used here are the relative values of feeding only for nights that aardwolves fed exclusively on *Trinervitermes*. This is because *Hodotermes* may feed during the day when it is too cold for them (or *Trinervitermes*) at night, and therefore their foraging is determined by a different temperature regime from that of *Trinervitermes*.
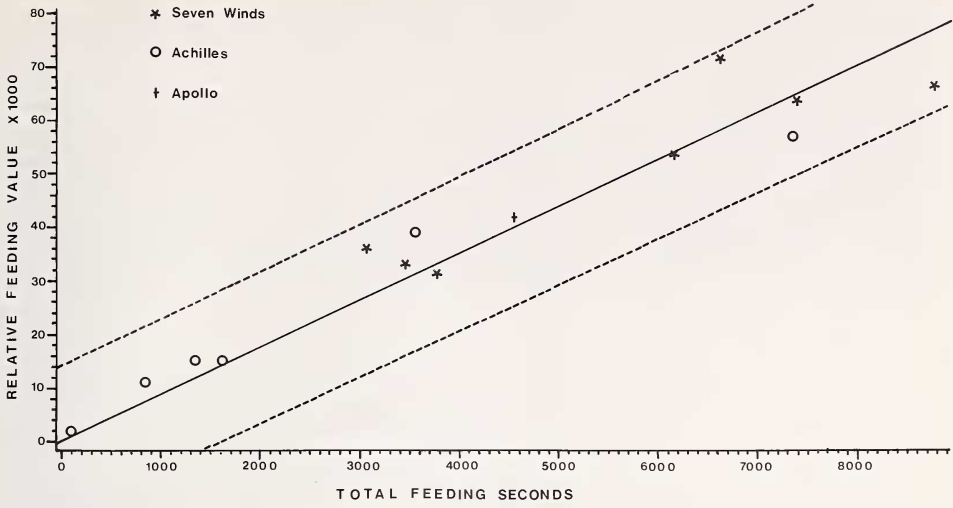
Fig. 2. Regression of the total relative feeding values per individual aardwolf against the total time it spent feeding during the all-night studies (r = 0.97, df = 13, p < 0.001; y = −293 + 0.118x; 95 % confidence limits are indicated)
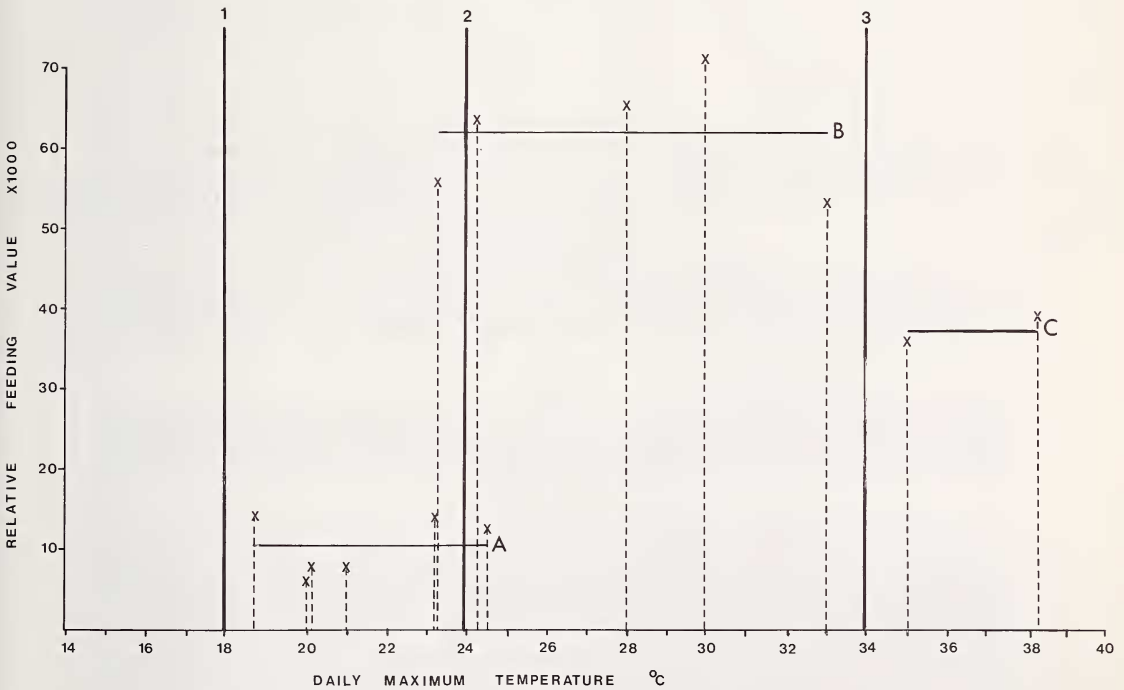

Fig. 3. Total relative feeding value per individual aardwolf plotted against the daily maximum temperature. Data are only from nights when aardwolves fed almost exclusively on *Trinervitermes* and when one animal was followed for its entire activity period. Threshold temperatures (1, 2 and 3), which determine termite activity, and the mean relative feeding values (A, B and C), are indicated

There are four distinct levels of feeding, and these appear to be determined by the effect of temperature on *Trinervitermes*. Below 18 °C there is no feeding. From 18–24 °C there is a low level of feeding. Above 24 °C there is a very much greater level of feeding, which drops again as the temperature rises above 34 °C. These results suggest that when the daily maximum is less than 18 °C, it gets too cold for the termites to forage in the evening. Above this temperature termites can forage for a few hours in the early evening, but it soon cools down and they return to their nests. A daily maximum of approximately 24 °C seems to be the turning point at which it no longer gets too cold for termite foraging. They can therefore forage all night, or at least until midnight. Thus there is a sudden increase in the termites available to aardwolves. As the temperature rises even higher, so termite activity declines again (NEL 1968; RICHARDSON 1985), and with it the feeding of aardwolves.
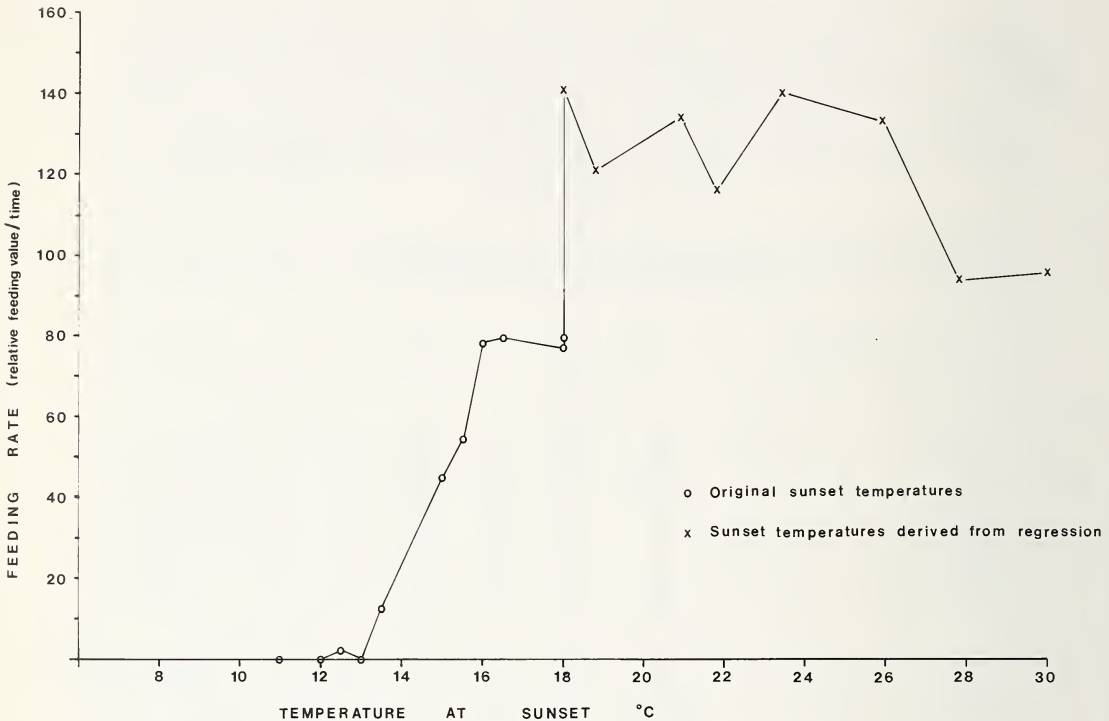

Fig. 4. Curve illustrating the dependence of aardwolf feeding rate (total relative feeding value per night/active foraging period) on the temperature at sunset. Data are only from nights when aardwolves fed almost exclusively on *Trinervitermes* and when one animal was followed for its entire activity period

In order to show that the pattern illustrated in Fig. 3 is a result of termite activity, and not simply a function of the time aardwolves spend feeding, the feeding rate is plotted against temperature at sunset in Fig. 4. The feeding rate is the total relative feeding value per night, divided by the time the aardwolves spent foraging. It therefore excludes any rest periods. Sunset temperature is used because this is the approximate time when the termites become active, and therefore should be an more accurate measure than the daily maximum. On most warm days the sunset temperature was not recorded, so these missing data were estimated using a regression of temperature at sunset against maximum daytime temperature. This is reasonable because these temperatures are very highly correlated ($r=0.97$, $df=17$, $p<0.001$).

This figure shows similar trends to Fig. 3, although it also suggests that termites become increasingly active as the temperature rises above 13 °C. This is presumably because there are more nests becoming active, so aardwolves have more chance of finding foraging termites.

The time, in relation to sunset, at which aardwolves were first observed to start feeding on *Trinervitermes* is plotted in Fig. 5. In this figure the only data used are for those days when aardwolves were followed from at least an hour before sunset. The earliest an aardwolf was seen to start feeding on *Trinervitermes* was 51 min before sunset, but it is clear that most termites become active in the last 15 min before sunset.

If cold is the major factor limiting the nocturnal foraging of the *Trinervitermes* during winter, then one would expect that once they have commenced foraging, these termites should continue for as long as possible to make the expedition energetically worthwhile. This was tested by comparing the times (relative to sunset) and temperatures at which aardwolves retired to their dens during winter, for nights when they had and had not fed on *Trinervitermes* (Table 4). Although the mean temperature at which aardwolves retired for the night was 1.3 °C lower when they had not fed on *Trinervitermes*, this difference was not significant. However, if they had fed the mean time of retiring was nearly two hours later, and this difference was highly significant ($p<0.001$).

The flexibility in aardwolf foraging behaviour during winter is further illustrated in Table 5, which summarises the data on total foraging periods (including rest periods) and the mean percentages activity for summer and winter. During the summer months aardwolves foraged for significantly longer periods ($p<0.001$) than in winter, but the percentage activity over the total foraging period was significantly lower ($p<0.05$). This was presumably because during winter, with the termites being active for a very limited period each night, aardwolves made maximum use of the opportunity to feed and therefore did not rest during the night. They did sometimes rest during the afternoon if
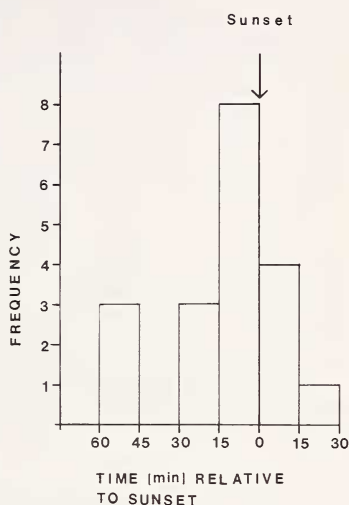

Fig. 5. Frequency of occasions when aardwolves started feeding on *Trinervitermes* during daylight, during the winter months

Table 4

Time and temperature at which aardwolves retired to their dens after they had, or had not fed on *Trinervitermes* during winter

	Mean Time After Sunset min	Std Dev	Range	Mean T °C	Std Dev	Range	n
Trinervitermes foraging	162.4	84.0	37–348	9.2	1.58	5.5–12.0	29
Trinervitermes not foraging	65.5	49.0	0–160	7.9	2.98	1.5–12.0	12

Mann-Whitney U test – Feed vs Not Feed:
Time: W = 727, n1 = 12, p < 0.001
Temp: W = 648, n1 = 12, p > 0.1

Table 5

Characteristics of foraging activity during summer and winter
Data excludes nights which were incomplete

Season	Foraging Period (h)		Overall % Activity		n
	Mean	Range	Mean	Range	
Summer	8.50	6.65–10.0	90.0	84.6–100	9
Winter[1]	3.50	1.10–5.92	94.4	32.3–100	30

[1] Excluding night when Achilles walked 24 km.
Mann-Whitney U test – Summer vs Winter:
Duration of active period: $W = 538$, $n1 = 9$, $p < 0.001$
Mean % activity per night: $W = 742$, $n1 = 9$, $p < 0.05$

they had become active earlier but found no *Hodotermes* foraging. They usually rested till about half an hour before sunset, then recommenced foraging.

There was however one exceptional night during June 1983, when a male, Achilles, walked 24 km in 10 hours and remained active until the temperature had dropped to zero – four hours after he had last fed on termites (Table 3). On this occasion he was involved in early mating season activities, and spent the whole night scent-marking his own and a neighbouring territory (RICHARDSON 1985). Because of this, the data for this day are not included in the above statistical analyses.

The general pattern of foraging activity throughout the year is illustrated in Fig. 6. During summer aardwolves generally became active about an hour after sunset and retired
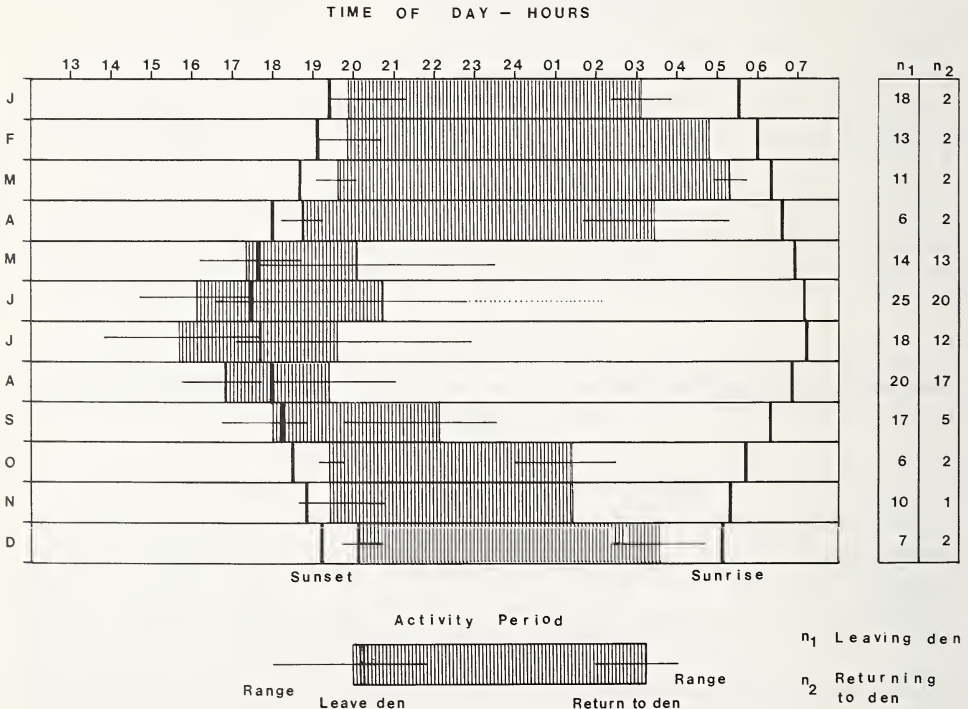

Fig. 6. Aardwolf activity periods during the year relative to sunset and sunrise. Data include only those observations when aardwolves were seen to emerge from, or retire to, their dens

before dawn. The winter pattern appears more flexible, with aardwolves retiring to their dens on some nights at times earlier than they had left the den on others. All these variations can be explained in terms of temperature and the activity of termites.

The total relative values of *Hodotermes* eaten per night during winter are illustrated in Fig. 7. There are a number of conclusions one can draw from this figure:

1. *Hodotermes* were sometimes active on days when it was too cold for *Trinervitermes* that night (daily maximum temperature <18 °C).
2. Within the temperature range that *Hodotermes* were observed to be active (daily maximum = 13–28 °C), they were still more frequently inactive than active. By contrast, *Trinervitermes* were always active in the evening if the daily maximum was over 18 °C.
3. Although the mean feeding value for 1984 was greater than that for 1983, this difference was not significant (Mann-Whitney U test; $W=124$, $n1=9$, $p>0.1$), nor was the frequency of days on which *Hodotermes* were active ($\chi^2=0.23$, $df=1$, $p>0.1$).

The general conclusion one can draw from this figure, is that although *Hodotermes* does sometimes provide an alternative food source for aardwolves during winter, it is not very reliable as such, nor does it provide the same amount of food per night as does *Trinervitermes* during summer.
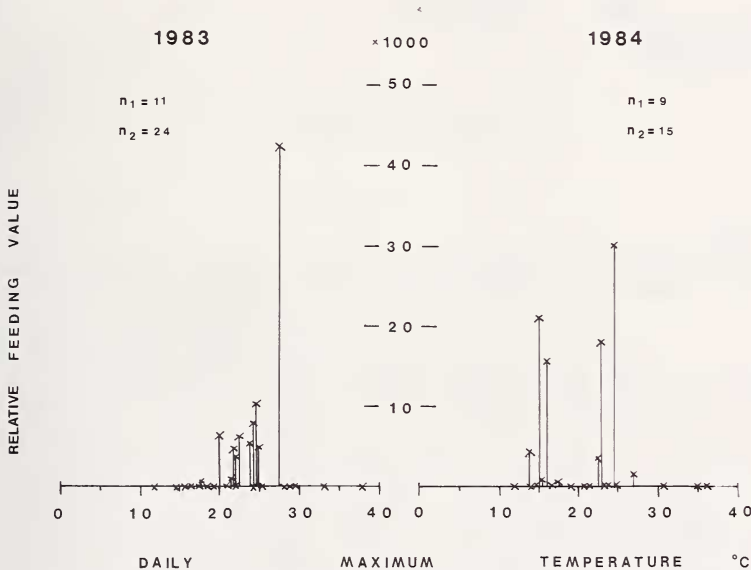

Fig. 7. Total relative values of *Hodotermes* consumed on days and nights during winter 1983 and 1984. Data include nights when aardwolves also fed on *Trinervitermes*, but are only for the days when one animal was followed for its entire activity period. The number of days on which *Hodotermes* were active (n1) and inactive (n2) are indicated

Faecal analysis

The mean percentages of *Trinervitermes* and *Hodotermes* present in the 136 aardwolf defaecations collected from middens are illustrated in Fig. 8. In all the samples, *Trinervitermes* and *Hodotermes* together accounted for almost the entire number of food items present, with other species of termites or insects comprising only traces. It is clear that, apart from during the winter months, *Trinervitermes* was practically the only item in the diet. This point is illustrated in Table 6, which shows that *Trinervitermes* comprised over
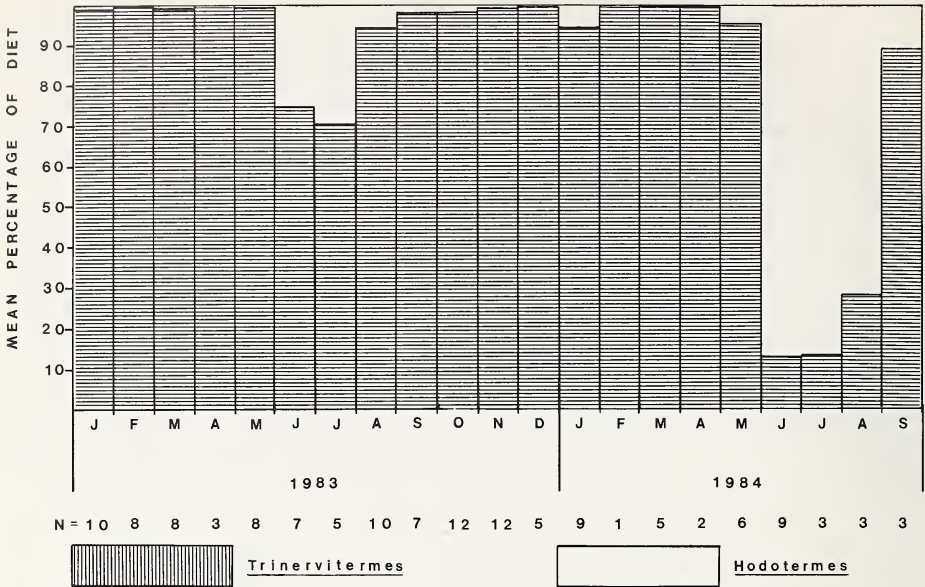
Fig. 8. Percentage occurrence of *Trinervitermes* and *Hodotermes* in 136 aardwolf defaecations collected over two years

99 % (by volume) of the diet in 75 % of the faeces collected and was totally absent in only 1.4 % of them.

It should be noted when interpreting Fig. 8, that it represents only the mean percentages of species present in each defaecation, and therefore does not take into account the volume of the faeces, which was generally much smaller during winter. Thus the overall proportion of *Hodotermes* in the annual energy budget is given an inflated value, although such a value may reflect its importance in winter when other foods are less available. In testing whether there was a significant increase of *Hodotermes* in the diet between 1983 and 1984, the data for June, July and August for the two years were used, comparing the frequency of faeces in which *Trinervitermes* or *Hodotermes* comprised the majority of the defaecation (Table 6). On this basis, there was a significant increase (p<0,001) of *Hodotermes* in the diet during 1984.

Table 6

Composition of 136 aardwolf defaecations collected from middens during 1983 and 1984

Defaecations	% volume of faeces containing *Trinervitermes*				Total
	0 %	> 50 %	> 99 %[1]	100 %	
Number	2	120	102	60	136
Percentage	1.4	88.2	75.0	58.8	–

[1] Traces of other species present.

Food consumption

Estimates of the total amount of *Trinervitermes* eaten by aardwolves per night and per year, are based entirely on the total relative feeding values and daily maximum temperature (Fig. 3). Because the results for the all night-studies showed that there were four distinct levels of feeding according to maximum temperature (T=<18 °C, 18<T=<24 °C,
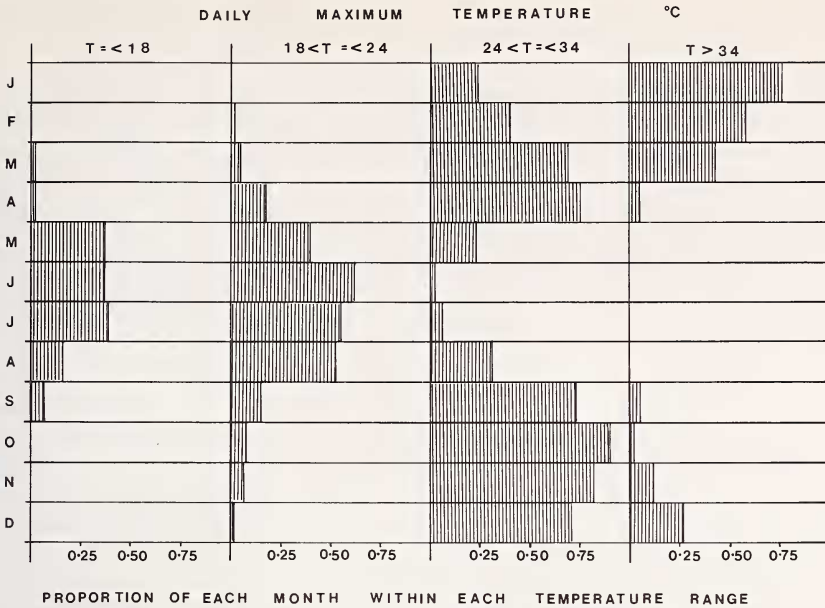
Fig. 9. Frequency distribution of four different temperature ranges per month. Data from Kimberley airport for the months October 1982 – September 1984

24<T=<34 °C, T>34 °C), the mean values for each temperature range were taken as representative values for the whole year. These values were then used to calculate the total *Trinervitermes* consumption per year, using the data on the daily maximum temperatures for the last two years of the study (September 1982–August 1984).

The frequency distribution of the four temperature ranges per month are illustrated in Fig. 9. The average monthly consumption of an adult aardwolf (Fig. 10A) was calculated by multiplying the frequency of these four temperature ranges per month by their respective relative feeding values (Fig. 3) then summing them. This figure (B) also illustrates the means of the original feeding values, recorded on nights when the entire activity period of an aardwolf was monitored. The mean values per month (B) and the values derived from the temperature distribution (A) are highly correlated (r=0.94, df=7, p<0.001) and their absolute values are also very similar, although the latter have lower peaks. Therefore these latter values (A) have been assumed to give a reasonable estimation of the *Trinervitermes* consumption of an adult aardwolf per year.

The mean consumption of *Hodotermes* per month is illustrated in Fig. 10B. It is noticeable that although the maximum values during winter may be very high, because of the relatively low frequency at which *Hodotermes* were active (Fig. 7), the mean values consumed per month were always lower than those of *Trinervitermes*. Thus although *Hodotermes* may, on some days, provide an alternative food source to *Trinervitermes,* on average it still provides less, and possibly helps little to alleviate the food shortage the aardwolf experiences during winter.

The estimation of the total number of *Trinervitermes* consumed per year is derived from the data above and the total number of termites counted in a day's faeces. The total dry weight of the complete day's faeces that was used for counting termites, was 853 g. Of this 10.8 g was sampled from five separate defaecations and 1,297 soldiers were counted. This gave a total of 99,400 soldiers and, using a mean soldier/worker ratio of 0.32 (RICHARDSON
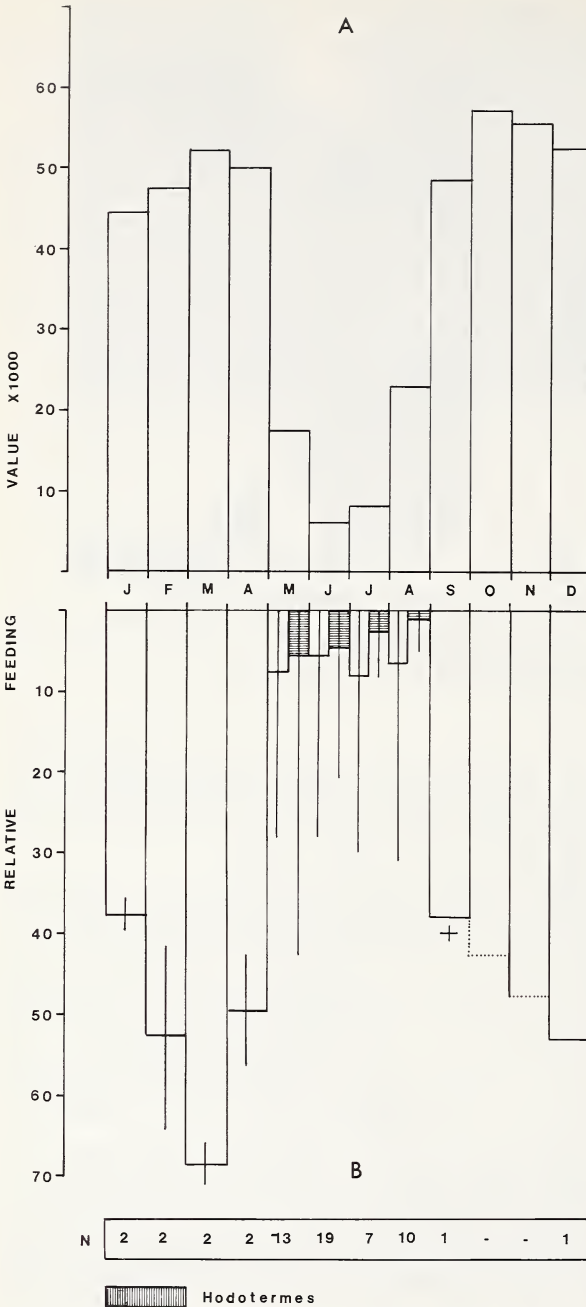
Fig. 10. Mean monthly consumption of *Trinervitermes* by an adult aardwolf during the year. A: data calculated from the temperature frequency distribution (Fig. 9). B: Mean values (with ranges) from nights when aardwolves were followed for the entire activity period. There were no data for October or November, and the September night was incomplete (only until midnight). Feeding on *Hodotermes* in winter is also indicated

1985), a grand total of 309,600 termites for the night.

This figure may appear remarkably high, however, it compares well with estimates from two other sources: (i) The total numbers of *Trinervitermes* in two aardwolf stomachs taken from individuals killed by motor vehicles were 249,000 and 270,000 (RICHARDSON 1985). (ii) On the night the faeces was collected the aardwolf (Apollo) fed on 396×2=792 termite patches (Table 4). This would give an average of 309,600/792=375 termites per patch. As on another occasion, over 500 termites were collected from two patches at which aardwolves had already fed, and over 4000 from some undisturbed patches (RICHARDSON 1985), this result is clearly quite possible.

A major assumption in the above calculation is that the total defaecations during a night (excluding the first of day 1 and taking the first of day 2) are all derived from the same night's feeding. It was not possible to prove this, but providing there are no great fluctuations in temperature, the amount of termites eaten on consecutive nights will be fairly constant. Similarly, the production of faeces should remain constant, so any 24 hour accumulation of faeces should give a fairly accurate estimate of food eaten during that period.

The faeces sampled above were collected on a night when the total relative feeding value was 41,600. As the total consumption per year is 14,100,000 (Fig. 10), this gives an estimate of:

$$\frac{14,100,00 \times 309,600}{41,600} = 104.9 = 105 \text{ million termites per year}$$

The average standing crop of *Trinervitermes* per territory is approximately 160 million termites (RICHARDSON 1985), and therefore each adult pair (without the cubs) consumes about 1.4 times the standing crop per year. Most termites, in fact most invertebrates, have a production/biomass ratio (P/B) of about three (WOOD and SANDS 1978). If this is also true for *T. trinervoides*, then it means that aardwolf predation alone could account for more than half the total production per year before even considering other energy losses, such as the production of alates, respiration and other mortality factors. This point illustrates the importance of these two species to each other and is discussed in another paper on aardwolf territoriality (RICHARDSON in prep.).

Body weight

The dependence of aardwolves on *Trinervitermes* as their main food source is illustrated by their decline in body weight during winter (Fig. 11). Although there are insufficient data for statistical analysis, there is a clear trend amongst both adults and cubs to lose weight during winter. The males were slow to gain weight after winter, but this is probably because they spent a great deal of time guarding cubs at the den while the female was away foraging (RICHARDSON 1985). These results do not take into account the weight of stomach contents. However, because most of the aardwolves were darted after they had been feeding for a few hours (they are most easily darted while they are feeding), there was probably little difference in the masses of their stomach contents, and certainly not sufficient to produce the 2.2 kg difference which was recorded for one male between May and September 1984.
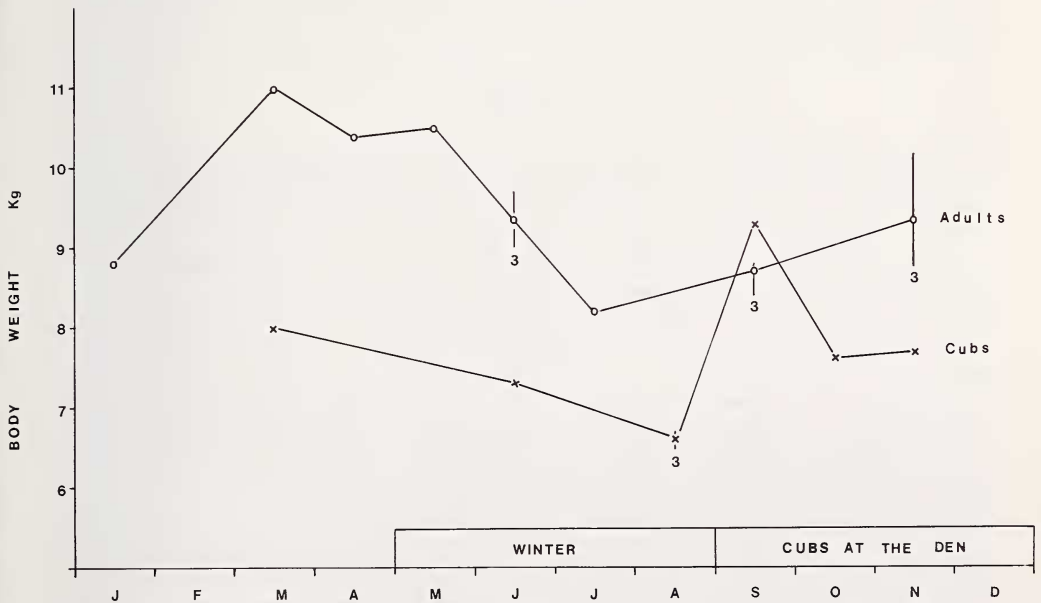

Fig. 11. Change in body weight of aardwolf adults and cubs during the year and in relation to periods of stress. Sample sizes and ranges are indicated

Cub survival

The survival of cubs born during the three years of the study is also regarded as being indicative of the feeding conditions. As cubs were first seen after they were about eight weeks old (RICHARDSON 1985), these data are taken to represent the numbers of cubs born – even although some may already have died. Cubs first start feeding on termites when they are about three and a half months old, but continue to suckle to a maximum age of five months (RICHARDSON 1985). The total number of cubs that survived for 12 months are presented in Table 7. All cubs survived for at least five months but those that died, disappeared during the winter. Significantly more cubs died during 1984 (p<0.001, n=6) than did in the previous two years (n=1). This last year was towards the end of what has been the worst drought in the past 60 years in South Africa (LUND 1983), and during this period there was a significant die-off of *Trinervitermes* mounds in certain parts of the study area (RICHARDSON 1985).

Table 7

Survival of cubs up to 12 months of age

	Survived 12 Months	Died
1981–3	10	1
1983/4	5	6

Fisher exact probability test: p < 0.001

These results show that winter must be a time of food stress for aardwolves. The adults appear to cope because, like many other mammals (HANKS 1981; KRUUK and PARISH 1983), they are able to utilise their fat reserves. By the end of summer aardwolves have considerable amounts of thick, yellow fat in the abdomen (ERASMUS pers. comm.; pers. observation). The cubs, however, may not be able to build up such large reserves of fat and may be more dependent than the adults on having food during the winter. In this respect it is interesting to note that there was a higher incidence of *Hodotermes* in the faeces of aardwolves during 1984 than there was in 1983, which may reflect a relative decrease in the availability of *Trinervitermes* during 1984. The combined effects of this, and of the winter, may have been the cause of the high incidence of cub mortality during this year.

Discussion

The above results confirm the importance of *Trinervitermes* (and secondarily *Hodotermes*) in the diet of the aardwolf as found by KRUUK and SANDS (1972) in East Africa, and COOPER and SKINNER (1979), BOTHMA and NEL (1983) and SMITHERS (1983) in southern Africa. However, in southern Africa none of these authors collected faeces on a regular monthly basis, and consequently did not notice the pronounced seasonal change which clearly relates to the cold temperatures prevalent during winter. Before pursuing this aspect, it is necessary first to consider an important physical difference between these termites, viz. pigmentation. In order to test their tolerances of ultra-violet radiation, HEWITT et al. (1972) conducted an experiment whereby they exposed workers of *T. trinervoides* and *Hodotermes* to two hours of direct sunlight. The experimental containers were maintained at a temperature of 20–25 °C during exposure and afterwards the termites were provided with ample drinking water. All the *Trinervitermes*, which are poorly pigmented, died within 24 hours of exposure. By contrast, only 21 % of the darkly pigmented *Hodotermes* died. This was to be expected, because *Hodotermes* are known to be most active during the daylight hours of winter and late autumn (NEL and HEWITT 1969). This therefore explains why *Trinervitermes* is never active by day (except occasionally in the late afternoon), and thus why *Hodotermes* features so prominently in the aardwolf's diet during winter.

Temperature is clearly the most important single factor influencing the availability of

Trinervitermes during the year. Being unable to tolerate direct sunlight *T. trinervoides* is almost exclusively a nocturnal forager. On nights when the temperature at sunset is <18 °C virtually no foraging takes place, and therefore, throughout most of winter (May–August), *Trinervitermes* is seldom available to aardwolves. This places considerable stress on these animals. This was evident from the weight loss experienced by all aardwolves during winter, and which probably caused the death of most of the cubs that died in their first year. These last two features suggest a great dependance by the aardwolf on *Trinervitermes* and also an apparent inability to feed successfully on alternative sources of food.

Although *Hodotermes* was an important substitute for *Trinervitermes* during winter, it was an irregular forager and therefore could not entirely make up the deficit. Furthermore, the aardwolf appears to be remarkably inefficient at feeding on insects other than harvester termites. During periods of low termite abundance aardwolves were occasionally seen to snap at locusts or antlions, but were never seen to eat substantial amounts of these insects. Thus the aardwolf appears to be so specialised at feeding on termites that it does not really regard other insects as food. This may be related to the extra energy expenditure required to catch more mobile insects, but is nevertheless in marked contrast to the bat-eared fox *Otocyon megalotis,* which feeds extensively on *Hodotermes* but is also most successful at catching various insects and arachnids, and digging up beetle larvae (NEL 1978; SMITHERS 1983; personal observation).

Some explanation for this situation can possibly be found in the extreme specialisation of the aardwolf's tongue, which is very large, flat and spatulate. The peculiarity of this tongue is reflected in its use. When feeding a captive aardwolf, SPINELLY (1970, p. 82) stated that "It seems to have great difficulty in feeding on what one would regard as 'normal' food because it uses its tongue, which is coated with sticky saliva, to pick up its food. The difficulties appear to be so great that it soon stops feeding altogether." SPINELLY overcame this problem by feeding the aardwolf small balls of mince held in the palm of her hand. Thus it would appear that the aardwolf is highly efficient at licking up small insects off the soil surface, but this is at the expense of being able to handle larger items of food.

As mentioned earlier, KRUUK and SANDS (1972) have postulated that it is its extreme specialisation for certain types of *Trinervitermes* that is responsible for the aardwolf being absent from Central and West Africa. In East Africa the western boundary of the aardwolf's distribution (SMITHERS 1983) approximately follows that of *T. bettonianus* (SANDS 1965), which is the aardwolf's main prey species in that region (KRUUK and SANDS 1972). In the savanna regions of West Africa, *T. geminatus* is a common harvester termite, so it is not immediately obvious why the aardwolf cannot survive there. The answer appears to lie in the foraging behaviour of the termites, and how well their harvesting habit (storing grass underground in nests) is developed.

All harvester termites prefer to collect mature or dry grass rather than green grass, which is toxic to some species (SANDS 1961; BOTHA and HEWITT 1978; OHIAGU 1979). Therefore, as green grass is most abundant during the wet season, this is when the true harvesters are least active. This is well documented for *Hodotermes* in southern Africa (NEL and HEWITT 1969), and for *T. geminatus* in West Africa (SANDS 1961; OHIAGU 1979). In northern Nigeria *T. geminatus* is largely inactive for three months during the wet season (July–September) and then again for four months during the cold dry season (November–February) (SANDS 1961). In southern Nigeria the wet season lasts very much longer, and virtually no harvesting takes place from May to October (OHIAGU 1979). Presumably the absence of harvester termites for six months of the year would place intolerable stress on the aardwolf (particularly the cubs), and thus prevent it from living in West Africa.

Although *T. bettonianus* and its ecological equivalents in southern Africa do harvest grass, they do so to a far lesser extent than *T. geminatus* and rely more heavily on browsing grass throughout the year (KRUUK and SANDS 1972). Because of this they cannot afford to remain inactive for extended periods, so they forage throughout the year except when

weather conditions inhibit it. They therefore provide a highly reliable food source – to such an extent that it has permitted the aardwolf to specialise almost exclusively on these few species.

Zusammenfassung

Nahrungsbedarf und saisonale Variabilität in der Ernährung des Erdwolfes Proteles cristatus in Südafrika

In Südafrika lebt der Erwolf *Proteles cristatus* fast ausschließlich von 2 Arten der an der Oberfläche ihre Nahrung findenden Grasschneidertermiten *Trinervitermes trinervoides* und *Hodotermes mossambicus*. Den größten Teil des Jahres ist der Erdwolf nachts aktiv und ernährt sich von *Trinervitermes,* die nur schwach pigmentiert ist und kein direktes Sonnenlicht verträgt. Wenn die Temperatur im Winter bei Sonnenuntergang <18 °C beträgt ist *Trinervitermes* nur eine spärliche Nahrungsquelle für den Erdwolf. *Hodotermes* ist dunkel pigmentiert und im Spätherbst und Winter hauptsächlich tagsüber aktiv. Auch der Erdwolf wird im Winter mehr zu einem Tagtier und ergänzt seine Nahrung durch Aufnahme von *Hodotermes.* Trotzdem leidet der Erdwolf noch unter Nahrungsmangel. Das beweist seine Gesichtsabnahme (bis zu 20 % des Körpergewichts), die bei allen Tieren im Winter auftritt. Nahrungsmangel ist sehr wahrscheinlich die Todesursache bei den meisten Jungen, die im 1. Lebensjahr eingehen. In ganz Afrika lebt der Erdwolf vorwiegend von einigen Arten der *Trinervitermes.* Es wird daher angenommen, daß das Vorkommen des Erdwolfs vom auftreten von *Trinervitermes* abhängt. Diese bestimmt die Verbreitung des Erdwolfes in Afrika.

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BUCHBESPRECHUNGEN

HAPPOLD, D. C. S.: **The mammals of Nigeria.** Oxford: Clarendon Press 1987. 402 S., zahlreiche Abb. und Tab., 10 Fototafeln, 112 Verbreitungskarten. Leinen £ 75.00. ISBN 0-19-857565-3

Der Autor, der viele Jahre im Sudan und in Nigeria verbracht hat, legt hier eine sorgfältige und inhaltsreiche Säugetierfauna vor, die er zugleich tiergeographisch-ökologisch analysiert. Auf 220 Seiten werden die 247 Arten Nigerias in systematischer Folge unter folgenden Gesichtspunkten behandelt: Allgemeine Verbreitung, Fundorte in Nigeria (dazu Karten und ein Verzeichnis der Fundorte mit ihren Koordinaten), Häufigkeit und Verteilung („Status"), Merkmale, Ökologie, Fortpflanzung und taxonomische Bemerkungen. Als Maße finden sich überwiegend nur kursorische Angaben zu den üblichen Körpermaßen, Gewicht und Schädellänge, teils als Mittel- und Extremwerte, oft auch nur „typische Werte" oder nur Extrema. Mit wenigen Ausnahmen beschränken sich die Beschreibungen auf äußere Kennzeichen. Zahn- und Schädelmerkmale werden nur ganz ausnahmsweise angegeben. Die innerartliche Variabilität wird nicht behandelt. Dafür gibt es Bestimmungsschlüssel zu den Familien, Gattungen und Arten, die im allgemeinen recht brauchbar erschei-